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Research Article

Compiling and analyzing the non-native flora of a megadiverse Neotropical country: a new catalogue for continental Ecuador

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Abstract

In this study, we provide a comprehensive and updated inventory of the non-native vascular flora of continental Ecuador and analyze its key biogeographic and ecological attributes to inform biological invasion management. We recorded 486 non-native wild plant taxa, 52% of which are naturalized and 48% casual. This inventory was primarily based on secondary data (published literature, scientific reports, and online databases) and enriched through fieldwork and expert consultations. It includes information on taxonomy, life form, lifespan, origin, first year of record, and spatial-temporal distribution. The most represented families were Poaceae (16%), Asteraceae (10%), and Fabaceae (9%). About 60% of the taxa originated from Asia and/or Africa, and 67% are herbs. The earliest introductions date back to the late 18th century, with an exponential increase beginning in ca. 1915. Only 13% of the taxa have a minimum residence time exceeding 125 years. The Andes accounted for the highest number of taxa (93%, including taxa shared with other regions). Nearly 80% of the non-native taxa have documented uses, most commonly ornamental (42%) and medicinal (38%). Naturalized taxa tended to have longer residence times and more frequently reported uses than casual ones, suggesting these traits may influence naturalization likelihood. Due to limited systematic sampling across the country, particularly outside the Central Andes, some spatial bias may exist. However, the integration of citizen science-derived data, a methodological innovation in our study, proved to be a promising approach for addressing knowledge gaps and improving detection efforts in regions with limited research capacity. Our findings offer a foundation for advancing the management of biological invasions in Ecuador

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through early detection, rapid response (EDRR), and species prioritization. Finally, we provide a practical, adaptable and replicable framework, based on citizen science and appropriate statistical analyses, for developing national inventories of non-native plant species in data-deficient countries.

Key words: checklist, first record, geographic origin, invasive alien plants, megadiverse country, Neotropic, pathways of introduction, residence time

Introduction

Biological invasions have become a significant threat to biodiversity, human health, and the economy. Invasive non-native species have contributed, solely or together with other drivers, to 60% of documented global extinctions (IPBES 2023); for a review, see Roy et al. (2024). Despite the known impacts attributed to invasive non-native species on the environment (e.g., Vilà et al. 2011; McCary et al. 2016; Zhou and Staver 2019; Torres et al. 2021; Roy et al. 2024), there is enough evidence to indicate a global increase in the number of new introductions (Seebens et al. 2017, 2021; Mormul et al. 2022), which may rise to over 200 species per year (IPBES 2023). The increase in non-native plants introduced as a consequence of human activity—whether intentionally (e.g., agriculture, forestry, horticulture) or unintentionally (e.g., contaminants) (Blackburn et al. 2011; van Kleunen et al. 2019), together with current rates of habitat loss and degradation, forest fragmentation, and land conversion, are transforming ecosystems (even in tropical regions) making them more susceptible and less resistant to biological invasions (Ackerman et al. 2017; Chong et al. 2021; Rojas-Sandoval et al. 2022).

First records of non-native vascular plant species have increased significantly during the 20th century. In fact, 37% of initial recorded global occurrences took place between 1970 and 2014 (Seebens et al. 2017). Additionally, it has been predicted that from 2005 to 2050, the number of non-native plant species will increase by 6% to 41% depending on the continent (excluding Pacific Islands; Seebens et al. 2017). In angiosperms, the doubling time of the number of new records is just 17 years (Mormul et al. 2022). Approximately 4% (≈ 13,168 species) of the total plant species on Earth (≈ 368,000 species) have become naturalized (i.e., established) outside their natural habitats (van Kleunen et al. 2015; Seebens et al. 2018). Thus, non-native plants are becoming a significant component of regional and national floras, in some cases with extremely high percentages, as is the case of New Zealand where non-native species make up nearly 90% of the country's plant diversity (Cáceres-Polgrossi et al. 2023).

Comprehensive and updated inventories of non-native species are essential for the development of regional prevention and management strategies (McGeoch et al. 2012; Lucy et al. 2016; Roy et al. 2019). Prevention, early detection, management, and control strategies require the development of an updated catalogue of non-native species to (i) restrict the entry of new non-native species through the creation of blacklists, decrees, and regulations; and (ii) prioritize and categorize species that have already been naturalized. In addition, understanding taxonomic, biogeographic (i.e., delimiting native and invaded ranges), and temporal trends (i.e., accumulation of first records) of introduced species in a given region contributes to producing updated databases and calculating estimates of introduction rates (see Pyšek et al. 2017; Seebens et al. 2017, 2021). Inventorying non-native

species is even more important considering Target 6 on invasive non-native species of the Kunming-Montreal Global Biodiversity Framework (adopted in 2022), which calls for "reducing the rates of introduction and establishment of other known or potentially invasive non-native species by at least 50 percent" (CBD 2022). Therefore, knowing the distribution of the invasive non-native species in a given region is a mandatory previous step to complying with this goal.

Local, regional, and national inventories have historically been more common in temperate and Mediterranean regions (Qian and Ricklefs 2006; Lambdon et al. 2008; van Kleunen et al. 2015), whereas they remain comparatively scarce in tropical areas, with the exception of certain island systems (Pyšek et al. 2017; Chong et al. 2021). Nevertheless, in recent years, there has been a growing body of research and comprehensive inventories of non-native plant species across tropical areas, including India (Khuroo et al. 2021; Wani et al. 2022), Mexico (Koleff et al. 2021; Ramírez-Albores and Badano 2021), Brazil (Silva et al. 2024; Zenni et al. 2024), Central America (Chacón-Madrigal et al. 2022; Rojas-Sandoval et al. 2023), the Caribbean (Rojas-Sandoval and Acevedo-Rodríguez 2015), tropical Africa (Ansong et al. 2019; Omer et al. 2021; Borokini et al. 2023), and Southeast Asia (Holmes et al. 2023; Sun et al. 2024). Within this expanding field of tropical biological invasions, our study contributes valuable data by focusing on Ecuador's mainland regions, which have traditionally received less attention. Although the Ecuadorian-owned Galapagos Islands have been the focus of extensive research on invasive non-native species (e.g., Gardener et al. 2013; Toral-Granda et al. 2017; Ballesteros-Mejia et al. 2021), comparable efforts in mainland Ecuador are still lacking, particularly in terms of comprehensive inventories of non-native vascular plants. For instance, in the global-scale Alien Species First Records Database v3.1 there are no records for mainland Ecuador (see Seebens 2023). Jørgensen and León-Yánez (1999) reported 595 non-native species of vascular plants in Ecuador (including Galapagos). Of these, 346 species were recorded as cultivated, and 249 as accidental introductions. A second attempt to compile a checklist of non-native species for Ecuador (excluding the Galapagos Islands) was published in the Global Register of Introduced and Invasive Species (GRIIS-Checklist of Introduced and Invasive Species – Ecuador), reporting 737 non-native species, of which 577 species were of vascular plants (Herrera et al. 2021). Despite being valuable, this work was a partial checklist that did not distinguish between wild and captive/cultivated plant taxa. Therefore, a more comprehensive inventory and catalogue of non-native plant species in Ecuador is still needed, even more considering that Ecuador is megadiverse, with part of the country's continental territory being included within two of the four biodiversity hotspots in South America; i.e., the Tropical Andes and the Tumbes–Chocó–Magdalena regions (Myers et al. 2000; Mittermeier et al. 2011).

The primary goal of this study is to provide a comprehensive and updated inventory of non-native vascular flora in continental Ecuador. However, beyond compiling a taxa list, we aim to address key ecological and biogeographical questions related to plant invasions in this megadiverse country. Specifically, we seek to: (1) characterize the taxonomic composition, life form, lifespan, geographic origin, and residence time of non-native taxa in continental Ecuador; (2) analyze the distribution patterns of non-native plant taxa across the country's bioregions and natural regions; (3) evaluate factors associated with the naturalization of non-native plant taxa by assessing the relationship between invasion status (casual vs. naturalized) and multiple ecological traits, including life form, lifespan, and economic uses;

and (4) determine whether certain variables, such as geographic origin or residence time, influence the likelihood of naturalization. To achieve these objectives, we integrate data from multiple sources—including herbarium records, scientific literature, global and regional databases, expert consultations, and own fieldwork—and apply statistical models to identify patterns and drivers of plant naturalization. Our findings enhance understanding of plant invasions in this tropical megadiverse country and provide a methodological framework that can be applied to develop national inventories of non-native species in other data-deficient countries. By incorporating citizen science (hereafter CS) data and appropriate statistical analyses, our approach offers a practical and adaptable framework for studying non-native species in regions where systematic surveys are logistically and financially challenging.

Methods

Study area

Ecuador lies in tropical South America between the Pacific Ocean and the Amazon basin, covering an area of ca. 250,000 km^2. Continental Ecuador is biogeographically divided into three principal bioregions: the Coastal, the Andean, and the Amazon (Fig. 1). The Andean Mountain range runs through the country from north to south, creating a barrier with a myriad of peaks exceeding 4,000 m (the highest mountain is Chimborazo, about 6,300 m). Coastal and lowland regions annually receive approximately 1,600 mm of precipitation, while the Andes receive less than 900 mm, and the Amazon basin precipitation averages around 4,600 mm (Morán-Tejeda et al. 2016). Average temperatures range from 12 °C in the mountains to 26 °C on the coast (Morán-Tejeda et al. 2016). The principal three bioregions of continental Ecuador are further subdivided into ten natural regions: Amazon, Andean Shrub, Chocó Tropical Rainforest, Deciduous Forest, Dry Shrub, Eastern Foothill, Eastern Montane, Paramo, Western Foothill, and Western Montane (Fig. 1). This classification is a simplification of the vegetation types of Ecuador (conformed by 71 natural ecosystems; Sierra et al. 1999) considering the environmental conditions (mean annual precipitation and temperature) and elevation (Ron 2020; available in https://bioweb.bio/faunaweb/amphibiaweb/RegionesNaturales).

The estimated total population of Ecuador is 16.9 million, with a rather low average population density of 68 people/km^2. The population, however, is very unevenly distributed over the country, with two particularly dense areas: Guayaquil and its metropolitan area, located on the coast with over 3 million inhabitants, and the Inter-Andean valleys, where the capital city, (Quito, with 2.6 million inhabitants) is located, as well as some of the largest cities of the country (Cuenca, Ambato, and Riobamba). In contrast, the Amazon bioregion is much less populated, with paved roads almost totally lacking. The Ecuadorian economy depends mainly on oil exports, although agricultural and aquacultural production also play a significant role in the country's economy. Ecuador exports products such as bananas, cocoa, flowers, and shrimp, among others (CCG 2022), which are mostly shipped through the port of Guayaquil.

Ecuador is the smallest of the 17 megadiverse countries (Ripple et al. 2017). With only 0.06% of the world's land area, it hosts approximately 18,600 taxa of vascular plants (Zapata et al. 2017). Despite its high biodiversity, land use change increases the vulnerability of Ecuador's species richness. The country has lost about 18% of

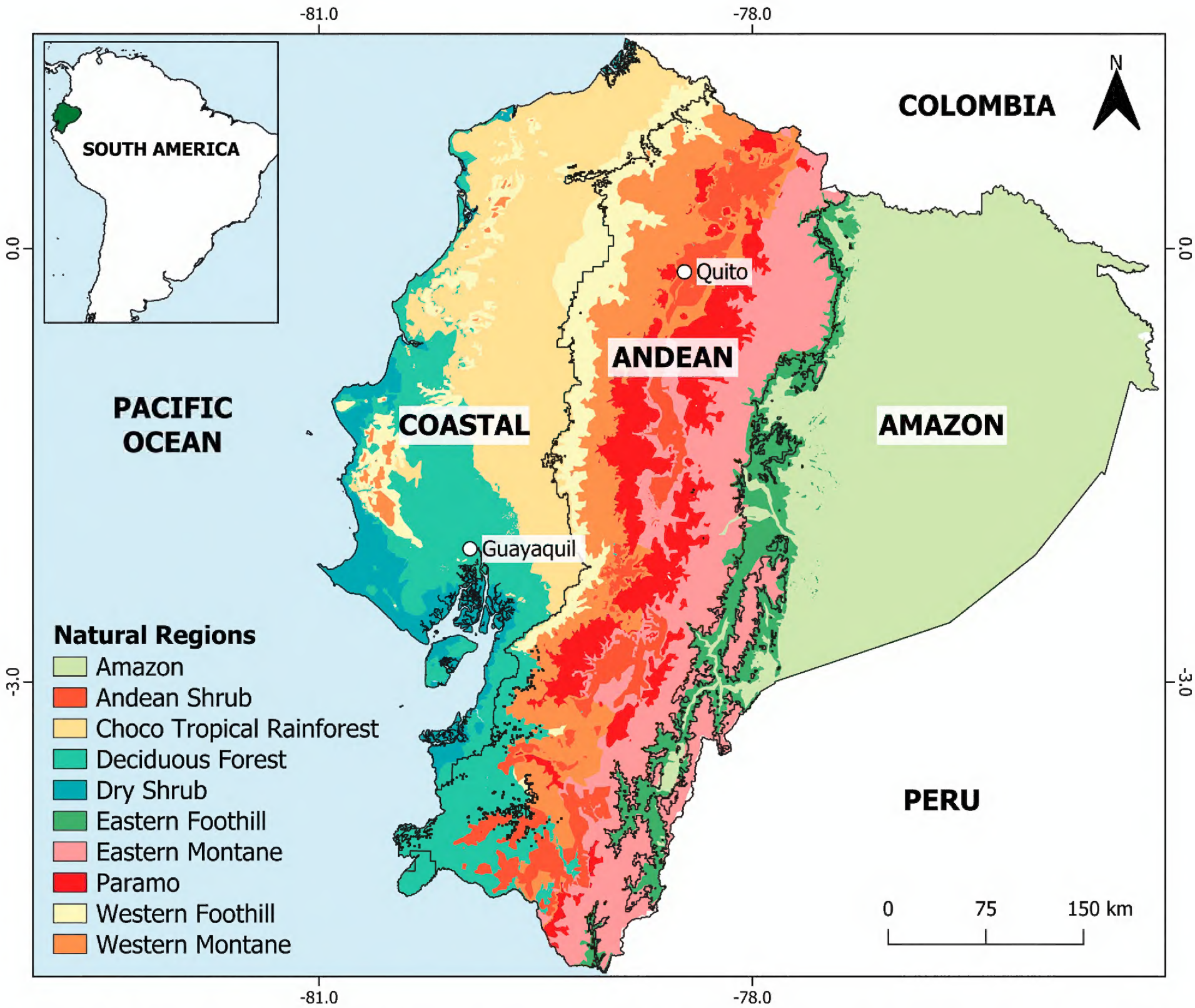

Figure 1. The three principal bioregions (Amazon, Andean, and Coastal), the ten natural regions, and the most populated cities (white dots) in continental Ecuador.

its forests between 1991 and 2018, mostly in the Coastal bioregion; at present, only 27% of the original forest cover remains in this bioregion, with percentages increasing to 48% for the Andean and 83% for the Amazon bioregions (Sierra et al. 2021).

Data collection and analysis

To compile our dataset (Step 1; Fig. 2), we first created a preliminary list of non-native plant taxa for continental Ecuador using the following main sources of information: (i) the global and national biodiversity databases, including the Global Register of Introduced and Invasive Species (GRIIS, Herrera et al. 2021, https://www.gbif.org/es/dataset/1df9467e-0c60-4e5a-a7b0-2b60bd6648ed), which served as a starting point to produce the catalogue; (ii) the Catalogue of Vascular Plants of Ecuador (W^3CEC) (Jørgensen and León-Yánez 1999) (http://www.tropicos.org/Project/CE; accessed from July 1, 2022, to December 31, 2023); (iii) the Global Naturalized Alien Flora database (GloNAF, https://glonaf.org/, van Kleunen et al. 2019); (iv) the Global Biodiversity Information Facility (GBIF; https://www.gbif.org/country/EC/summary; accessed from July 1, 2022, to December 31, 2023); (v) the CABI

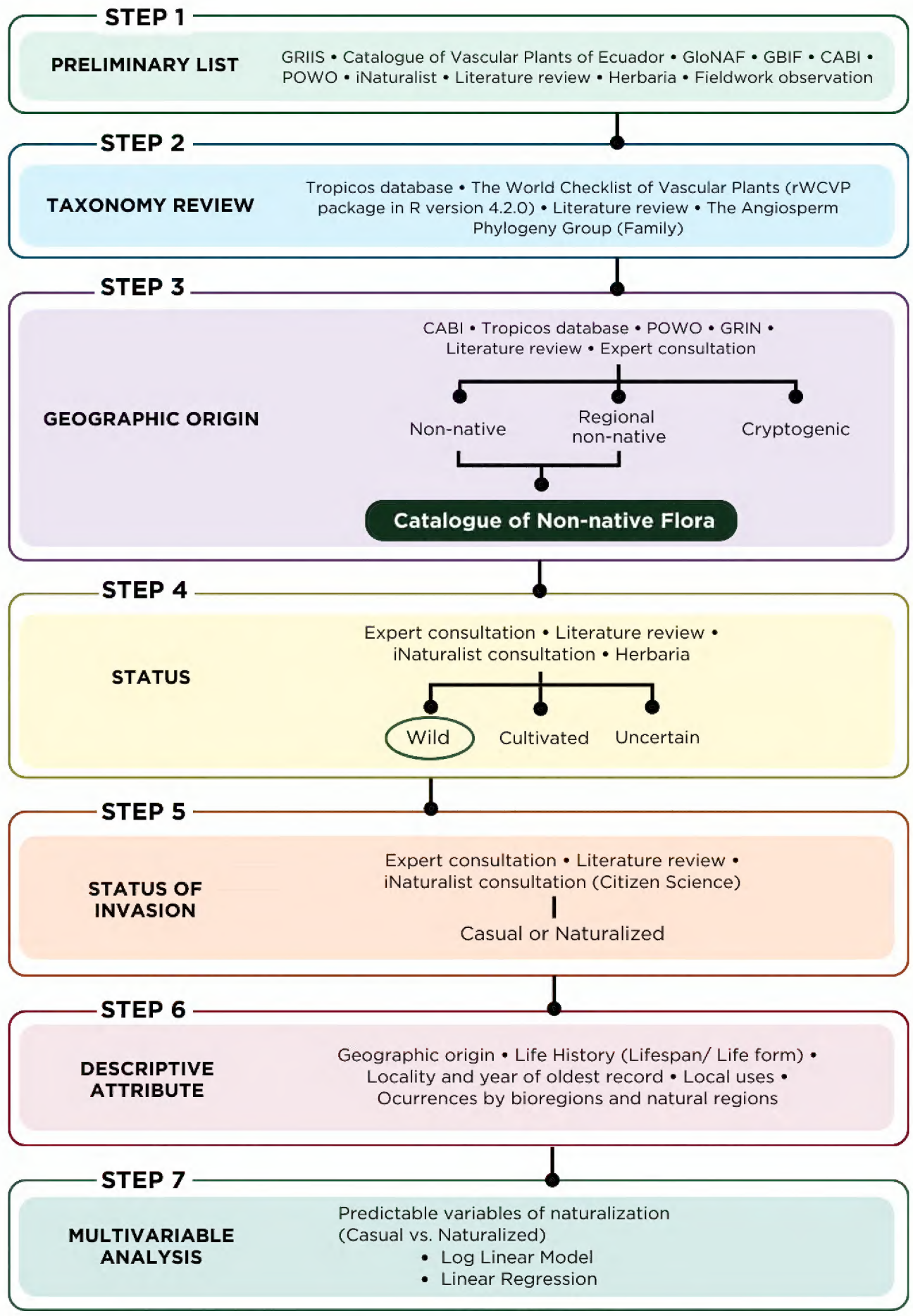
STEP 1
PRELIMINARY LIST
GRIIS • Catalogue of Vascular Plants of Ecuador • GloNAF • GBIF • CABI • POWO • iNaturalist • Literature review • Herbaria • Fieldwork observation
STEP 2
TAXONOMY REVIEW
Tropicos database • The World Checklist of Vascular Plants (rWCVP package in R version 4.2.0) • Literature review • The Angiosperm Phylogeny Group (Family)
STEP 3
GEOGRAPHIC ORIGIN
CABI • Tropicos database • POWO • GRIN • Literature review • Expert consultation
Non-native
Regional non-native
Cryptogenic
Catalogue of Non-native Flora
STEP 4
STATUS
Expert consultation • Literature review • iNaturalist consultation • Herbaria
Wild
Cultivated
Uncertain
STEP 5
STATUS OF INVASION
Expert consultation • Literature review • iNaturalist consultation (Citizen Science)
Casual or Naturalized
STEP 6
DESCRIPTIVE ATTRIBUTE
Geographic origin • Life History (Lifespan/ Life form) • Locality and year of oldest record • Local uses • Ocurrences by bioregions and natural regions
STEP 7
MULTIVARIABLE ANALYSIS
Predictable variables of naturalization (Casual vs. Naturalized)
• Log Linear Model
• Linear Regression

Figure 2. Methodological framework to construct and analyze the catalogue of non-native flora.

Compendium (Centre for Agricultural Bioscience International; https://www.cabi.org/; accessed from July 1, 2022, to December 31, 2023), (vi) the Plants of the World Online database (POWO; https://powo.science.kew.org/; accessed from July 1, 2022, to December 31, 2023); and (vii) the iNaturalist CS web portal (https://www.inaturalist.org/; accessed from July 1, 2022, to December 31, 2023) (Fig. 2).

This preliminary list was supplemented with data extracted from literature review, which included research articles, books, grey literature, relevant floras, and anthropology papers or books discussing the documented uses of plants in Ecuador. These documents were retrieved through scholarly search engines and databases such as ISI Web of Knowledge, Scopus, SciELO, Google Scholar, and CABI Compendium. Search queries were conducted in both English and Spanish, with no restriction on publication year, using the following strings: "Introduced plants," "Exotic plants," "Invasive plants," "Non-native plants", "Alien plants", and "Ecuador." Additional data was collected from academic (PhD, MSc, or undergraduate)

dissertations and project reports sourced from repositories of public and private institutions in Ecuador. Herbarium collections were also searched through databases and platforms such as Tropicos® of the Missouri Botanical Garden (https://www.tropicos.org) and GBIF (https://www.gbif.org). Finally, we also relied on our own observations during fieldwork (which were often recorded through iNaturalist).

The preliminary list was further screened for taxonomic name standardization (Step 2; Fig. 2) using the list of accepted names from the Tropicos® database (available at https://www.tropicos.org) and The World Checklist of Vascular Plants (WCVP, Govaerts et al. 2021) using the "rWCVP" package (Brown et al. 2023) in R version 4.2.0 (R Core Team 2021). WCVP is one of the most authoritative checklists for vascular plants, and it is used to feed the Plants of the World Online (POWO) webbase. For those species that differed in taxonomic classification between the two databases (Tropicos® and WCVP), an exhaustive search in the specialized literature was carried out. To provide insight into the taxonomic composition of the non-native flora of continental Ecuador, each taxon was classified by order, family, and genus. Families have been assigned according to APG IV (2016). Step 2 (Fig. 2) allowed us to obtain a preliminary list without duplicates, synonyms, or uncertain records.

To confirm that all taxa in this list are non-native (Step 3; Fig. 2), we gathered information on the native geographic range for each plant taxon in CABI Compendium (https://www.cabidigitallibrary.org/journal/cabicompendium), Tropicos® database, POWO (Plants of the World Online; https://powo.science.kew.org/), and GRIN (Germplasm Resource Information Network; https://npgsweb.ars-grin.gov/gringlobal/taxon/taxonomysearch). We compared the information obtained in these databases and, for those species where the information on their native range was contradictory, we conducted an exhaustive search in the specialized literature. We categorized species with no certainty of being native or non-native in continental Ecuador as cryptogenic, which were excluded from the analysis. Taxa native to a particular region in Ecuador but growing in secondary habitats (i.e., apophytes) in other regions of the country beyond their natural distribution area were classified as regional non-native taxa. Hybrids were also considered because they are a sizable part of the ornamental flora, which is widely acknowledged as a primary source of naturalization and even invasion (Pergl et al. 2016). Only those hybrids with at least one non-native parental species were considered. Infraspecific taxa (i.e., subspecies) were only considered when they were solid taxonomic entities (unequivocally accepted subspecies or even when they are accepted at the species rank by many) and morphologically distinguishable from other subspecies.

At this point, and before entering Step 4 (Fig. 2), we launched a six-month national consultation process with more than 100 local experts. Participants were asked to review the list, as well as proposing additions or deletions. Although many contacted experts specialized in native flora, 18 botanists with substantial experience in non-native taxa actively contributed and are co-authors of this study. These experts represent herbaria and research institutions from Ecuador's three main bioregions: Andes, Amazon, and Coast. The consultation involved multiple rounds of email correspondence, video calls, and interactive workshops. To ensure consistency in classification criteria and foster a shared conceptual framework, the process began with a national webinar (on February 8, 2024). This session was led by one of the co-chairs of the IPBES Assessment on Invasive Alien Species, Dr. Aníbal Pauchard, along with one of the study's authors. The webinar introduced key invasion biology concepts—such as non-native, naturalized, and invasive species—and

provided guidance to harmonize classification standards among participants from different regions and institutions. This capacity-building component was essential to align criteria and improve the reliability of expert-based validation.

The six-month consultation period culminated in the creation of the catalogue of non-native flora for continental Ecuador (Fig. 2). The Step 4 (Fig. 2) consisted of classifying each non-native taxon into one of three categories: (i) wild (with at least one occurrence outside cultivation); (ii) cultivated; or (iii) uncertain (for those taxa where it could not be corroborated whether their occurrences are cultivated or outside cultivation). The local experts of the consultation process were also asked on the wild/cultivated status of the taxa. In addition, we conducted an extensive literature search (by using the same sources of previous steps) with the following descriptors: "Cultivated [Species scientific name]", "Naturalized [Species scientific name]", "Invasive [Species scientific name]", "Wild [Species scientific name]", and "Ecuador". iNaturalist played a prominent role in distinguishing between cultivated and wild plant species. This popular tool, in addition to being the world's largest CS website, enables us to mark the records as "cultivated." However, if the iNaturalist user forgets to mark the "cultivated" tag, the images included in every record often make it possible to see whether the observed plant is wild or cultivated (Vargas et al. 2022). Nonetheless, the status of all doubtful occurrences was confirmed by asking each user who uploaded them (iNaturalist allows direct contact between users; López-Guillén et al. 2024). Additionally, for some records we consulted other tools that offer panoramic or 360-degree imagery (such as Google Maps and Google Street View), which helped verify the surrounding environment and confirm whether the species was growing under cultivation or in the wild.

Based on expert knowledge (of the consultation panel), CS and literature review—and considering only the species that were reported as growing in the wild—we categorized the plant taxa in the next level of the classification (Step 5; Fig. 2): (i) "casual" when they are capable of surviving in the wild and even to occasionally reproduce outside cultivation, but eventually die out because they do not form self-replacing populations and rely on repeated introductions for their persistence, and (ii) "naturalized" when they produce self-sustaining and viable populations, without direct intervention by humans, or despite human intervention (see complete definitions of these two terms in Pyšek et al. 2004; Blackburn et al. 2011; Rojas-Sandoval and Acevedo-Rodríguez 2015; Roy et al. 2024; Soto et al. 2024). We did not classify non-native plant taxa as "invasive" due to the lack of data on dispersal and impacts. As with the classification of plant taxa as wild or cultivated, iNaturalist has played a central role in further categorizing wild taxa as casual or naturalized.

Finally, the following descriptive attributes for the wild non-native taxa (casual and naturalized) were added to the dataset (Step 6; Fig. 2):

i. Geographic origin. The native area was defined using the "World geographical scheme for recording plant distributions" (WGSRPD; Brummitt 2001). For analytical purposes, we employed the first level of the WGSRPD, which consists of nine biogeographical global regions: North America, South America, Europe, Africa, Asia-Temperate, Asia-Tropical, Australasia, Pacific Islands, and Antarctica. The origin of hybrids was categorized based on the origin of their parental species.
ii. Life history. Non-native plant taxa were categorized based on two life history traits: lifespan (annual, biennial, or perennial) and life form (aquatic, herb, shrub, tree, succulent, or vine). Palms were included in the tree category. Assignment of species to these categories is based on our observations as well

as on Ecuadorian floras, scientific literature, or databases, such as the Catalogue of Vascular Plants of Ecuador. For those species where this information was not available, we used the floras from their native areas.

iii. Locality and year of oldest record. We used the "minimum residence time" (Pyšek and Jarošík 2005) as a proxy to indicate the latest possible date of introduction of each species to Ecuador. Information was obtained from several sources, including scientific literature, databases (including Tropicos® and GBIF), and iNaturalist (from which we extracted the date of the oldest available record). Also, an exhaustive search of herbarium sheets was carried out in several online and offline herbaria. For those cases where the first record was based on a herbarium specimen, a picture of the voucher was requested to corroborate the veracity of the data. We excluded records with ambiguous identifications, missing dates, or lacking georeferencing information. The majority (89%) of records were obtained from herbaria, 7% from CS, 3% from scientific publications, and 1% from living specimens in botanical gardens. We used the year and region of the first record to generate accumulation curves of the first records on the national scale and for the three bioregions of continental Ecuador (Amazon, Andean, and Coastal). When a record did not provide any specific place, the region was categorized as "undetermined" and was excluded from regional accumulation curves. Also, to find any relation between residence time and the invasion status we divided the residence time into four categories: old (<1900), mid-term (1900–1949), recent (1950–1999), and very recent (>1999).

iv. Local uses. To identify the potential reasons for the introduction and/or expansion of each non-native wild taxon, we conducted a comprehensive search to record its uses in continental Ecuador. Information sources to determine species uses included scientific papers, books (e.g., "Enciclopedia de las plantas útiles del Ecuador" [Encyclopedia of useful plants of Ecuador] by de la Torre et al. 2008), personal blogs, and other non-scientific websites. Uses were classified into nine categories: (i) ornamental (including plants cultivated in gardens, parks, and avenues); (ii) forestry (encompassing plants utilized for soil restoration, afforestation, and living fences); (iii) medicinal (for humans and/or animals); (iv) ancestral (plants used in rituals, ceremonies, and cultural activities); (v) food crops (for human consumption); (vi) animal food (including forage and fodder for domestic animal food); (vii) industrial (for textile and industrial purposes); (viii) fuel (such as wood for heating or cooking); and (ix) toxic (plants used for their toxic properties) (adopted from Pyšek et al. 2002).

v. Occurrences by bioregions and natural regions. We estimated the number of non-native plant taxa in continental Ecuador for each of the three bioregions and each of the 10 natural regions. For this, we downloaded occurrences of non-native plant taxa in the wild (excluding cultivated taxa) from both the GBIF and iNaturalist. Also, records in research articles, books, and grey literature were consulted, as well as personal observations. A preliminary database was generated with at least the following information for each record: (i) taxon name, (ii) coordinates, (iii) occurrence year, (iv) political province, and (v) source of record. This database was uploaded to QGIS 3.28.3 where occurrences with spatial errors (outside continental Ecuador or in the sea), duplicated, and/or without coordinates or locality, were deleted. Finally, each record was updated with the natural region and bioregion. We normalized the taxa number by the area of each bioregion and natural region.

After cataloging non-native plant taxa, we conducted a comprehensive analysis exploring their frequencies across multiple dimensions, including taxonomy (e.g., families), life form, lifespan, geographic origin, residence time, and distribution patterns (covering both bioregions and natural regions) (Step 7; Fig. 2). To evaluate the relationship between invasion status (i.e., casual and naturalized), the analyses were carried out only on a national scale due to a lack of information on the bioregional scale (Andes, Amazon, and Coast). We used Pearson's chi-squared test of independence for (1) all life forms, (2) life forms divided into herbs (both terrestrial and aquatic) and other life forms (shrub, tree, herb, succulent, vine), (3) lifespan, (4) overall use (any use = yes; no use = no), and (5) residence time. Interactions between these variables were tested using log-linear models of the frequency of values for all combinations of categories. We compared an independent model (all additive terms) with a full model (multiplicative terms between status and the other four variables) and intermediate models summarizing association with each combination of one, two, or three variables. We tested model assumptions by diagnosing the residuals and compared models using the Akaike information criterion (AIC). We fitted a logistic regression to determine what uses or regions of origin of the non-native plant taxa are associated with naturalization. The status of the non-native plant taxa in the dataset was formatted to a binary response (non-native plants scored 1 if they were classified as naturalized, while all casual taxa scored 0), and employed different overlapping uses as predictors.

Results

Non-native plant taxa in continental Ecuador

We documented 1,255 non-native and five regional non-native taxa in continental Ecuador (for a total of 1,260 taxa). Most of them (770 taxa, 61%) were cultivated (i.e., not having any record as escaped from cultivation), while 0.3% (four taxa) had an unknown status. This comprehensive catalogue includes 486 non-native taxa (and regional non-native) occurring in the wild (39% of the total of non-native taxa). These included 478 species, three subspecies, and five hybrids (Suppl. material 1). Of the 486 non-native wild plant taxa, we found that 231 taxa (48%) have been recorded exclusively as casual, and 255 (52%) have at least one report as naturalized at the scale of continental Ecuador.

The non-native plant taxa occurring in the wild in continental Ecuador belonged to 32 orders, 87 families, and 333 genera. Poaceae (80 taxa, 16%), Asteraceae (47 taxa, 10%), and Fabaceae (42 taxa, 9%) were the families with the largest numbers of non-native plant taxa in continental Ecuador (Fig. 3). Forty-eight families were represented by only one or two non-native taxa. The genus with the highest number of non-native taxa was *Kalanchoe* (nine taxa, 2%), followed by *Eragrostis*, *Rumex*, *Digitaria*, and *Solanum* (seven taxa each, 1%), while 61% of the genera (295) were represented by fewer than two taxa.

Geographic origin

Most of the non-native flora of continental Ecuador came from multiple regions (i.e., a combination of regions) rather than a single region (Fig. 4A). The Old World (i.e., temperate and tropical Asia plus Africa and Europe) followed by North and

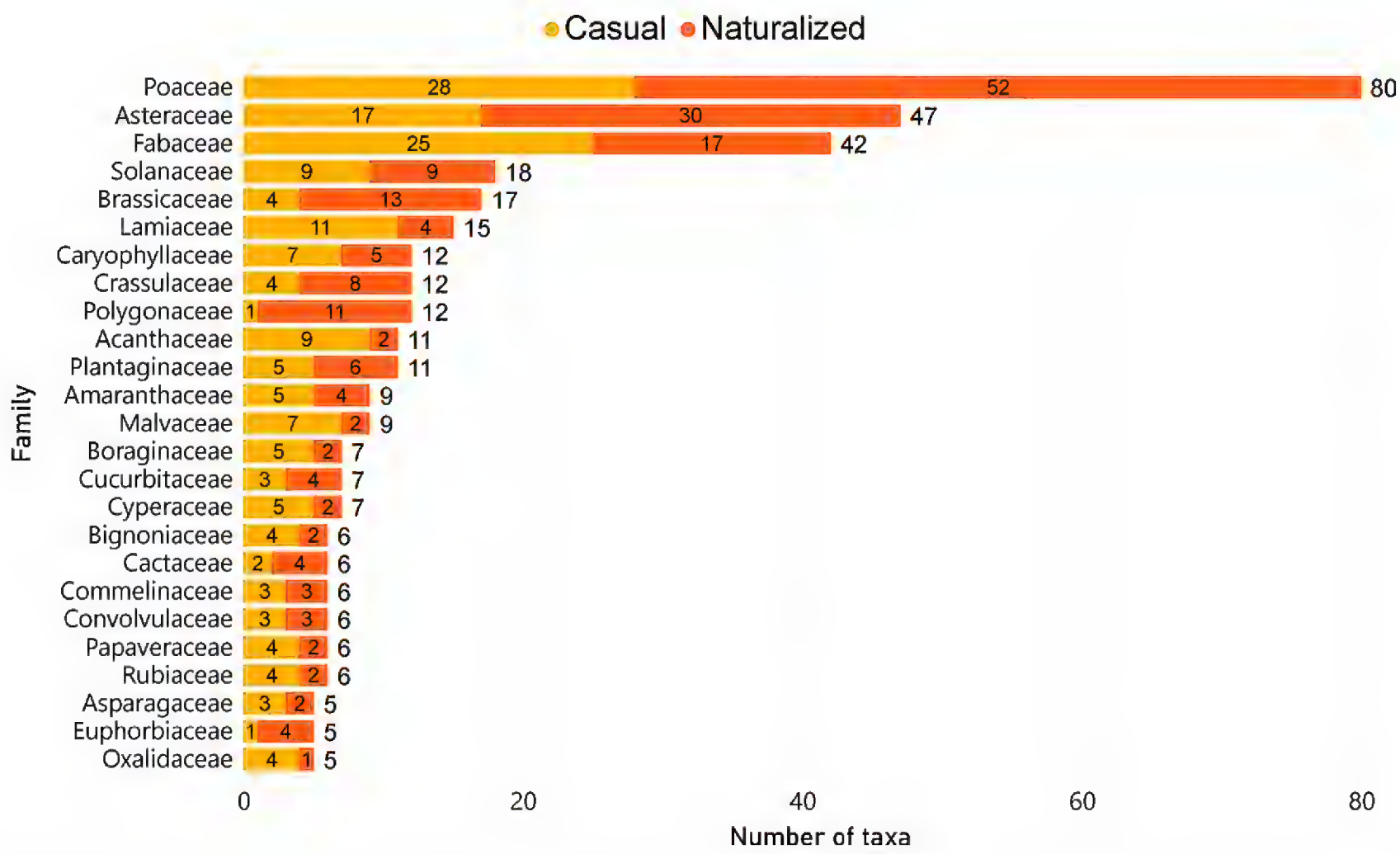

Figure 3. Number of non-native plant taxa of the most diverse plant families of continental Ecuador. For each family, taxa are categorized as either casual or naturalized.

South America were the two most significant sources of non-native taxa of continental Ecuador, with 16% (78 taxa) and 13% (61 taxa), respectively (Fig. 4A). As single regions, Africa and South America contributed the most (10% and 9%, respectively; Fig. 4A). Summing all possible combinations in which each of the eight WGSRPD regions is included (i.e., among the 49 possible cases included in the x-axis of Fig. 4A), these regions ranked as follows (Fig. 4B): Asia-Temperate (22%), Africa (21%), Asia-Tropical (17%), Europe (14%), South America (10%), North America (8%), Australasia (4%), and Pacific Islands (2%).

Occurrences by bioregions and natural regions

In terms of bioregional distribution, the majority of non-native wild plant species were recorded in the Andean region (451 taxa, 93%), followed by the Coastal (253 taxa, 52%) and Amazon regions (182 taxa, 37%) (Fig. 5A). A similar pattern emerged when the number of taxa was normalized by the area of each bioregion, with the Andes showing the highest value (0.005 taxa/km^2), followed by the Coastal (0.004 taxa/km^2) and Amazon regions (0.002 taxa/km^2) (Fig. 5A). Some species were shared between regions, while others were exclusive to a single region. A total of 191 taxa were exclusive to the Andes, 26 taxa were only found in the Coastal region, and three taxa were solely present in the Amazon region (see Fig. 5A). There were 135 non-native plant taxa shared among all three bioregions (see Fig. 5A).

Of the natural regions in continental Ecuador, Andean Shrub showed the highest number of non-native plant taxa (368 taxa) (Fig. 5B), while the Dry Shrub had the fewest (136 taxa) (Fig. 5B); the Andean Shrub also showed the largest number of non-native plant taxa detected exclusively in a single region (25 taxa) (Fig. 5B). When the number of taxa was adjusted by the area of each natural region, the Andean Shrub also showed the highest value (0.033 taxa/km^2; Fig. 5C), while the Amazon and Chocó Tropical Rainforest had the lowest values (0.002 taxa/km^2 and 0.006 taxa/km^2,

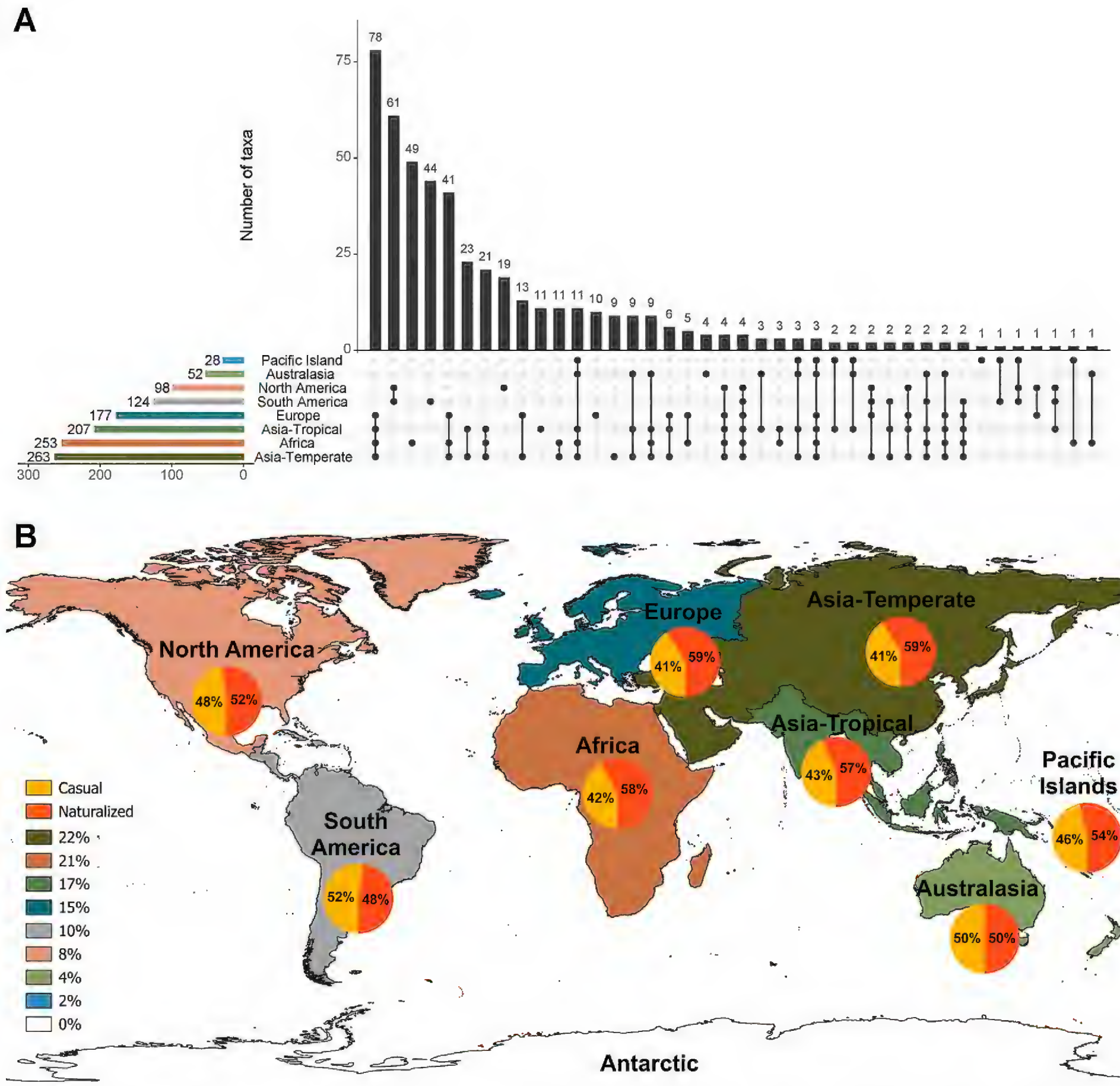

Figure 4. A. The total number of non-native taxa in continental Ecuador by all possible combinations of geographic origins; **B.** The percentage of the contribution of each WGSRPD geographic region to the total number of non-native taxa in continental Ecuador. The pie charts show the percentage of casual and naturalized non-native taxa per continent. Percentages were calculated considering all recorded origins for each species (i.e., a given species can come from more than one continent).

respectively; Fig. 5C). Interestingly, although the Dry Shrub had the fewest total taxa, it ranked second in number of taxa per square kilometer, with 0.017 taxa/km^2 (Fig. 5C).

We found that most of the taxa that come from Europe (175 out of 177; i.e., 99%), Asia-Temperate (244 out of 263, 93%), and Africa (233 out of 253, 92%) were present in the Andean region, while few taxa from Europe occurred in the Coastal (41 out of 177, 23%) and Amazon (31 out of 177, 18%) bioregions (Fig. 5D).

Lifespan and life form

Over half (52%) of the non-native wild plant taxa in continental Ecuador had a perennial lifespan (252 taxa), while the other 48% of the taxa could complete their life cycle in one or two years (annuals and/or biennials, 234 taxa) (Fig. 6A). In terms

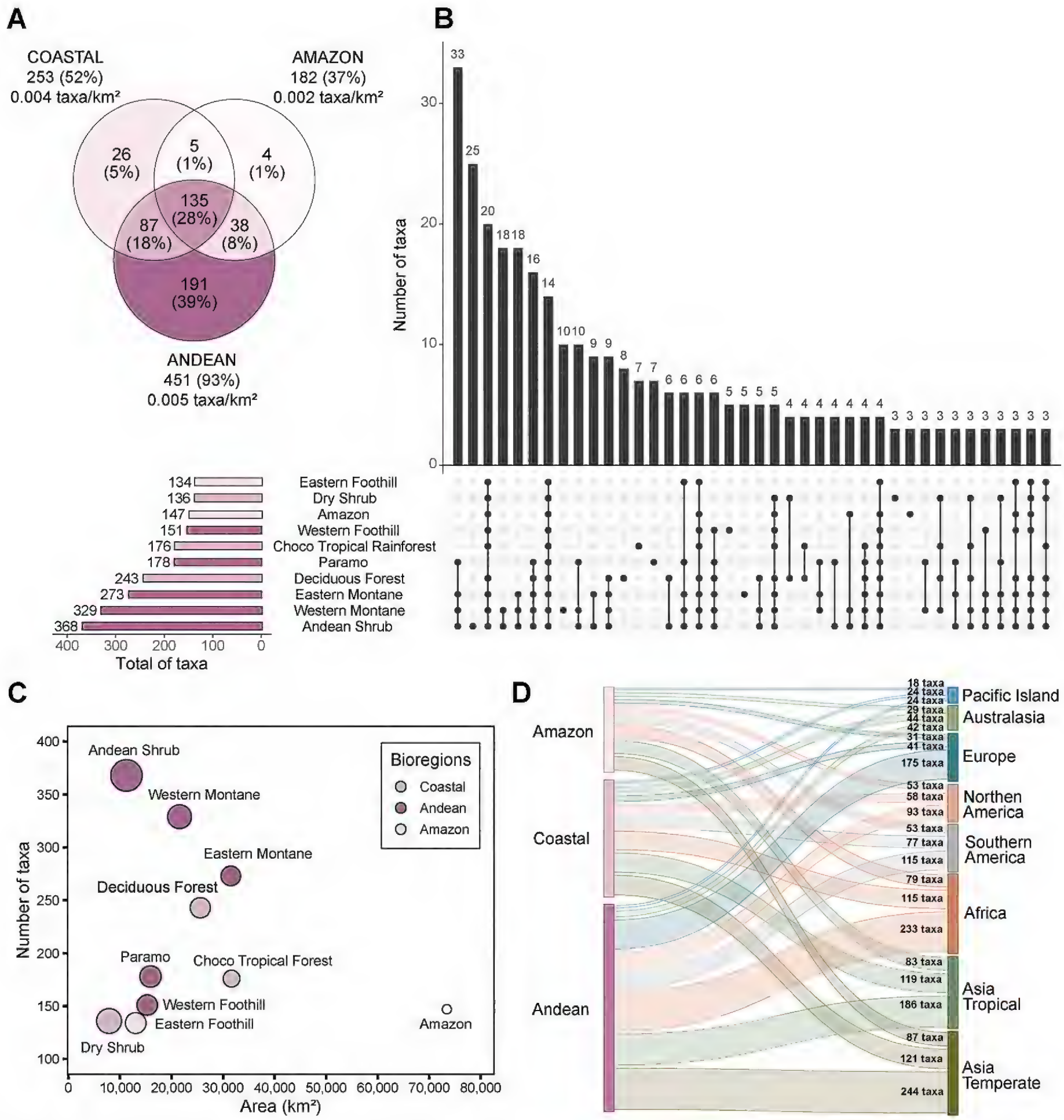

Figure 5. **A.** Number and percentage of non-native wild taxa found in each of the three Ecuadorian bioregions and those shared by two or three bioregions; **B.** Number of non-native taxa found in each of the 10 natural regions of Ecuador and those shared by two or more of these regions; **C.** Relationship between the number of taxa and area (km²) across different natural regions. Each point represents a natural region, with the size of the circle indicating the normalized taxonomic richness (number of taxa/km²); **D.** Number of non-native taxa present in the Amazon, Andean, and Coastal bioregions by geographic origin (please note that the origin of a given species can include more than one of the eight possible WGSRPD regions; see Fig. 4).

of life form, there was a dominance of herbs (67%, 325 taxa), followed by shrubs (11%), trees (8%), vines (8%), succulents (5%), and aquatic herbs (1%) (Fig. 6B).

Residence time and accumulation of first records

Most of the non-native wild taxa (423 taxa, 87%) have been present in continental Ecuador for less than 125 years. About half of these (203 taxa, with 37% classified as casual, and 63% as naturalized) showed a residence time between

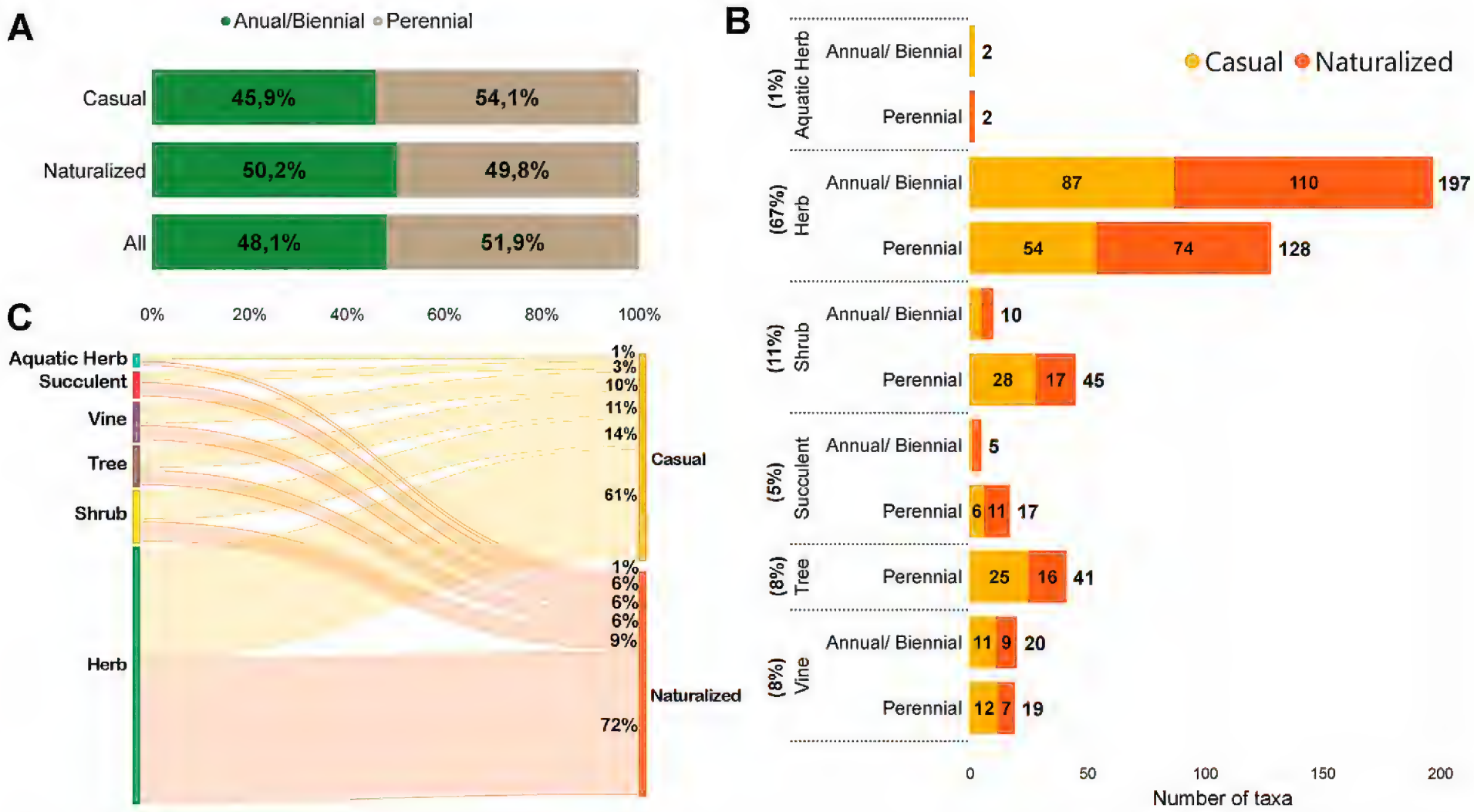

Figure 6. Total, naturalized, and casual taxa according to their lifespan and life form: **A.** Percentage of total, naturalized, and casual taxa by lifespan; **B.** Number of taxa per lifespan and their corresponding life form; **C.** Percentage of casual and naturalized taxa by life form (and, within each category of life form, by lifespan).

75 and 125 years, being classified as mid-term, while 66 taxa (of which 64% were classified as casual and 36% as naturalized) have been in continental Ecuador for less than 25 years, and are classified as very recent (Fig. 7A). A positive association was found between the proportion of naturalized species and residence time (very recent, recent, and mid-term), with a slight decrease in this proportion for older taxa (Fig. 7B). There was a continuous increase in the cumulative number of first records from 1799 (represented by two herbarium specimens, of *Anacardium occidentale* L. and *Heliotropium indicum* L., without reported location or region) to 1910 for the non-native wild species (Fig. 7C); from this year on, the cumulative number of first records increased exponentially, mostly for the Andean region (Fig. 7D). For the present time, the accumulation curve of first records appeared to have reached a plateau (i.e., showing signs of stabilization) for the Coastal region, but not the Andean or Amazon bioregions (Fig. 7D). Most of the first records (322 taxa, 66%) were from the Andean region, with the earliest occurrence recorded in 1817 (Fig. 5B), followed by the Coastal region (116 taxa, 24%), where the earliest record was for 1836 (Fig. 7D). A significantly lower percentage (11 taxa, 2%) of first records was detected in the Amazon region, with the earliest record dating back to 1962 and increasing from 1985 onwards (Fig. 7D). The biogeographical region associated with the first record could not be determined for 37 taxa (8%) (including the earliest ones; data not shown). Six species had the oldest records in continental Ecuador, reaching back more than two centuries (*A. occidentale* L. and *H. indicum* L. in 1799, *Sphenoclea zeylanica* Gaertn. in 1800, *Oplismenus burmanni* (Retz.) P. Beauv. in 1802, *Ageratum conyzoides* L. in 1817, and *Oxalis corniculata* L. in 1824).

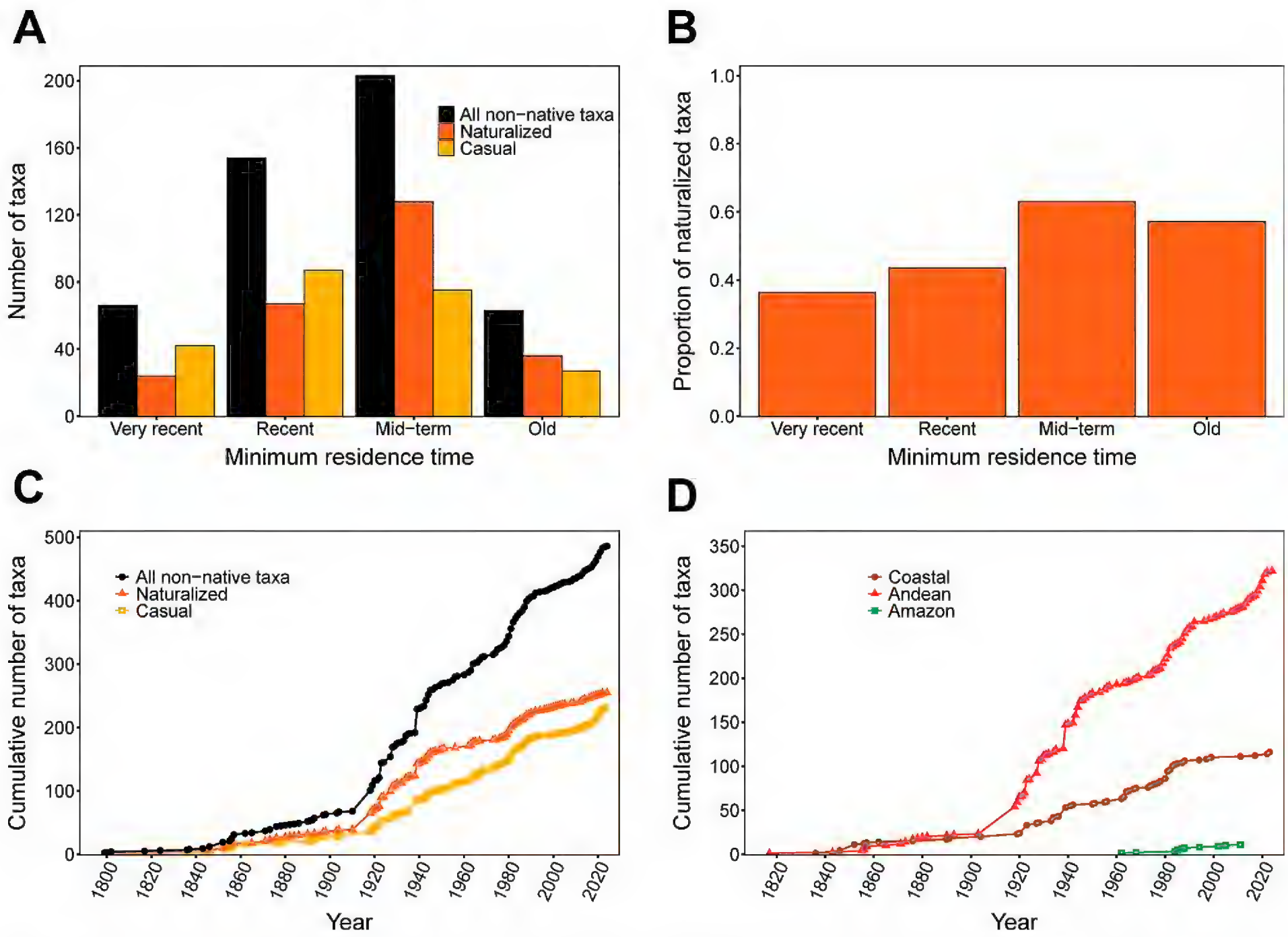

Figure 7. Accumulation of first records of non-native wild plants. **A.** Minimum residence time for all taxa recorded in continental Ecuador, categorized as old (<1900), mid-term (1900–1949), recent (1950–1999), and very recent (>1999); **B.** Proportion of naturalized taxa in each category in continental Ecuador; **C.** Accumulation curve of first records in the wild for continental Ecuador; **D.** Accumulation curves of first records in the wild for the Coastal, Andean, and Amazon bioregions.

Local uses

We recorded local uses for 385 (ca. 79%) wild taxa in continental Ecuador. The most frequent uses of these taxa were ornamental (202 taxa, 42%) and medicinal (187 taxa, 38%). Fewer than 40% of the useful taxa were employed as food crops, for ancestral purposes, as animal food, or in forestry (Suppl. material 1). When the casual and naturalized taxa were considered separately, the main uses were also ornamental (202 taxa; casual: 41% and naturalized: 42%) and medicinal (187 taxa; casual: 33% and naturalized 44%) (Suppl. material 1).

Casual vs. naturalized

We did not detect significant effects of any geographic origin on the proportions of casual and naturalized taxa in the logistic regression model (Suppl. material 2). There were also no statistical differences in lifespan between casual and naturalized taxa (χ^2 = 0.74, df = 1, P = 0.39) (Suppl. material 3, Fig. 6A). In contrast, statistical differences were detected between casual and naturalized taxa with respect to life form, as herbs were over-represented in naturalized taxa (χ^2 = 12.81, df = 4, P = 0.012) (Suppl. material 3, Fig. 6C). When the life form was simplified to only

two categories, herbaceous and non-herbaceous, we also found significant differences (χ^2 = 6.26, df = 1, P = 0.012; Suppl. material 3); naturalized herbs were significantly (P < 0.05) over-represented compared to casual herbs; in contrast, casual non-herbs (shrubs, trees, and vines) were significantly over-represented.

Broadly speaking, the proportion of naturalized taxa tended to increase with residence time (Fig. 5D). There was a non-random distribution of categories of residence time (χ^2 = 21.50, df = 3, P < 0.0001; Suppl. material 3) among casual and naturalized non-native flora in continental Ecuador. Among the non-native naturalized taxa, those with a mid-term residence time (1900–1949) were significantly over-represented (P < 0.05; Suppl. material 3). In contrast, casual taxa were significantly (P < 0.05; Suppl. material 3) over-represented in the recent (1950–1999) and very recent residence times (since the 2000s; Suppl. material 3). In taxa with an old residence time, there were no significant differences between the number of naturalized and casual taxa (P < 0.05; Suppl. material 3).

There were no statistical differences in local uses reported between casual and naturalized taxa (χ^2 = 2.11, df = 1, P = 0.14). A logistic regression of the status (0, casual; 1, naturalized) with life form, residence time, and local uses as explanatory variables found that only forage use had a significant effect increasing the likelihood of the species being naturalized. Ancestral use also had a large positive effect although it was not significant, probably due to the correlation between ancestral use and residence time (the other significant variable in the regression model).

We used log-linear models to test the assumption of independence of these effects (life form, lifespan, local use, and residence time). Comparison between several log-linear models suggested that the full model (AIC = 422.78) had better support than an independent model (AIC = 440.81). However, the best model included only three variables associated with naturalized status: residence time, life form, and local use (AIC = 421.92; Table 1, Suppl. material 4), suggesting that lifespan did not have a true association with naturalized status when the other three variables are included. The apparent effect of herbs was, nevertheless, not significant in the log-linear model, suggesting a frequency effect (more herbs than other life forms in the list) rather than a real relationship. In contrast, local use and residence time were both significantly associated with naturalization status: the fact that a species had a recorded use in continental Ecuador was significantly linked to its naturalization status and similarly, the frequency of naturalization increased linearly with residence time categories (very recent < recent < mid-term < old).

Discussion

Number of non-native plants in Ecuador: Why are there so few non-native wild plant taxa in Ecuador and other megadiverse Neotropical countries?

Our updated catalogue of non-native plants (1,260 taxa, with 770 occurring exclusively as cultivated plants, 486 taxa with populations in the wild, and four taxa with an unknown status) in continental Ecuador doubles the number of taxa previously reported in the Catalogue of the Vascular Plants of Ecuador (595 taxa, 346 as cultivated and 249 as wild; Jørgensen and León-Yánez 1999) and the GRIIS checklist (577 taxa without distinguishing between cultivated and wild species; Herrera et al. 2021). Herein we are reporting the presence of nearly five hundred non-native plant taxa that grow spontaneously and represent 2.6% of the flora of Ecuador,

Table 1. Summary of the selected log-linear model based on a multidimensional contingency table with interactions between invasion status and life form, use and residence time, and the additive effect of lifespan. Coefficients (beta) with their 95% confidence interval (CI), value of the *z* statistic and P-value are included.

Variable	Beta (95% CI)	Z	P
Intercept	-0.29 (-2.10, 0.86)	-0.41	0.69
status (ref = Casual)			
Naturalized	-2.04 (-4.24, 0.16)	-1.95	0.05
form (ref = Aquatic Herb)			
Herb	1.99 (0.81, 3.80)	2.74	0.006
Shrub	0.89 (-0.35, 2.73)	1.19	0.23
Succulent	0.03 (-1.43, 1.96)	0.04	0.97
Tree	1.31 (0.04, 3.16)	1.73	0.08
Vine	0.44 (-0.82, 2.29)	0.59	0.56
use (ref = No)			
Yes	0.71 (0.41, 1.04)	4.45	<0.001
residence (ref = Very recent)			
Recent	0.52 (0.15, 0.90)	2.72	0.007
Intermediate	0.44 (0.06, 0.83)	2.23	0.03
Old	-0.35 (-0.85, 0.13)	-1.43	0.15
lifespan (ref = Annual/ Biennial)			
Perennial	-0.20 (-0.39, -0.01)	-2.07	0.04
status by form			
Naturalized, Herb	1.17 (-0.98, 3.33)	1.15	0.25
Naturalized, Shrub	0.37 (-1.84, 2.57)	0.35	0.73
Naturalized, Succulent	1.73 (-0.57, 4.05)	1.55	0.12
Naturalized, Tree	0.48 (-1.75, 2.71)	0.45	0.65
Naturalized, Vine	0.68 (-1.55, 2.91)	0.64	0.52
status by use	0.45 (-0.01, 0.91)	1.94	0.05
status by residence			
Naturalized, Recent	0.48 (-0.11, 1.09)	1.57	0.12
Naturalized, Intermediate	1.21 (0.63, 1.80)	4.07	<0.001
Naturalized, Old	0.85 (0.14, 1.57)	2.33	0.02

considering that the native flora of continental Ecuador comprises approximately 18,600 taxa (Zapata et al. 2017). This percentage is much lower compared with other regions, particularly from the Northern Hemisphere; for example, 17.8% in Italy (Galasso et al. 2024), 21.6% in Norway (Sandvik et al. 2019), or 37.7% in Czech Republic (Pyšek et al. 2022). Nonetheless, the rate of Ecuadorian non-native/native taxa reported in this study is not much smaller than those reported in other countries of tropical America (including the regional megadiverse countries), such as the Caatinga area of Brazil (4.6% in an area of 800,000 km^2; Almeida et al. 2015), Colombia (1.7%; recalculated from raw data of Bernal et al. 2016), Mexico (5.5%; obtained through the most recent non-native flora of the country [Ramírez-Albores and Badano 2021], the total flora as recorded in "efloraMEX" [https://efloramex.ib.unam.mx/]), and Central America (7.5%; Rojas-Sandoval et al. 2023).

The pattern of low richness of non-native plants is congruent with the hypothesis of biotic resistance to non-native species in species-rich communities, particularly those of tropical latitudes (Rejmánek 1996; Teo et al. 2003; Mungi et al. 2021). However, this hypothesis remains controversial (e.g., Chong et al. 2021) and, certainly, other factors may be responsible for the low percentages of non-native flora in Ecuador and other Neotropical countries. Perhaps the simplest explanation is the

much shorter tradition of floristic research on non-native plants —several countries lack or just have preliminary checklists (e.g., the megadiverse countries of Peru and Venezuela, but also Bolivia and Paraguay; Speziale et al. 2012), which may stem from two factors: (1) the generalized low investment in R&D, which is fully translated into a much better knowledge of plant diversity (Amano and Sutherland 2013; Meyer et al. 2016); and (2) the lack of interest by the local scientific community in non-native plant species (Pauchard et al. 2004). A second reason is the comparatively lower gross domestic product (GDP) of Neotropical countries. Economic development is a key driver of biological invasions, as it increases the probability of non-native species introduction and establishment through disturbances and trade (Hulme 2009; Pyšek et al. 2010; Amano et al. 2016; Rojas-Sandoval et al. 2020). Finally, the comparatively much higher parts of Neotropical countries being lands managed and/or controlled by indigenous peoples (Garnett et al. 2018) might also have played a role. Globally, indigenous peoples' lands host up to 30% fewer non-native species than other lands (Seebens et al. 2024), which may stem from the fact that indigenous peoples are generally aware of invasive non-native species in their lands, even having active policies of control and response (Ens et al. 2015; Reo et al. 2017).

Patterns of non-native flora in Ecuador

Nearly half of the non-native plant taxa detected have been recorded exclusively as casual (48%). This high percentage of casual plants, though similar to or even higher than those reported for other Neotropical countries (e.g., 32% for Central America [Rojas-Sandoval et al. 2023]; 19.8% for megadiverse Mexico [Villaseñor and Espinosa-García 2004]), is much lower than those reported for countries with a high tradition of documenting their non-native plants (e.g., Belgium [74.6%; Verloove et al. 2004] or the Czech Republic [68.8%; Pyšek et al. 2022]). In the latter countries, extensive fieldwork has been carried out by the authors of their non-native flora catalogues, often consisting of repeated inventories over time. In Ecuador and many other Neotropical countries, however, checklists often rely exclusively on revision of the existing literature, with very little *ad hoc* fieldwork. In such circumstances, casual taxa, which are more likely to have fewer occurrences and lower population sizes—and, importantly, survive only temporarily in the new region—can easily go unnoticed.

The top three families of non-native taxa in Ecuador—Poaceae, Asteraceae, and Fabaceae—align with global trends (Pyšek 1998) and findings in other parts of the Neotropics, including the megadiverse countries [Mexico (Ramírez-Albores and Badano 2021), Brazil (taking into account only naturalized plants; Zenni 2015), and Central America (Rojas-Sandoval et al. 2023)]. Surprisingly, the genus *Kalanchoe* (Crassulaceae) has the highest number of non-native taxa in continental Ecuador (nine out of 486). This is likely an artifact resulting from a recent national-scale review (Vargas et al. 2022), suggesting that the number of taxa in other genera may be underestimated due to the lack of studies specifically focused on Ecuador's non-native flora. In the recently published study of the non-native flora of Central America, the genus *Kalanchoe* has an even lower number of representatives (eight, ranking 10th in the list of most speciose genera) among a much larger non-native flora (1228 taxa; Rojas-Sandoval et al. 2023).

In continental Ecuador, most non-native plant taxa originate from the Old World (particularly temperate and tropical Asia and Africa), which account for over two-thirds of the 486 recorded taxa. These results are strikingly almost identical to those

reported for the non-native flora of Central America (Rojas-Sandoval et al. 2023) but also similar to other megadiverse Neotropical countries; Asia and Africa are the main sources of both the non-native flora of Mexico (46%; calculated from raw data of Ramírez-Albores and Badano (2021) and the invasive non-native plant taxa of Brazil (about 65%; Zenni 2014)). The prevalence of African and Asian taxa reflects climatic similarities with Ecuador's tropical and subtropical climates, a key factor in non-native plant establishment (Feng et al. 2016; Fristoe et al. 2023). Climate similarity would also explain why the European species are not predominant in Ecuador despite the early exchange of flora with Europe during the colonial period, which is also the norm with the other Neotropical areas for which we have data (Central America and the megadiverse Brazil and Mexico). Only in the Ecuadorian Andes does the European flora exhibit a notable presence (Fig. 5D), likely due to climatic similarities between the Andes and certain regions of Europe (they share the temperate climate Cfb of the Köppen-Geiger climate classification; https://koppen.earth/).

The lack of plant taxa introduced before the Spanish colonization (i.e., archaeophytes) in the present catalogue can be attributed to the nonexistence of written records prior to the Spanish colonization in the 16th century, a common issue in Neotropical countries. In Mexico, for example, the first documented introductions, despite being about three centuries older than that of Ecuador (Ramírez-Albores and Badano 2021), were also linked to the Spanish conquerors. Though generally a minor component of the non-native floras of the world, archaeophytes can still be a sizeable component of them (e.g., in the Czech Republic archaeophytes represent about one-quarter of the total non-native flora (Pyšek et al. 2022). Adopting a conservative approach, all the species would be neophytes (i.e., those introduced after 1500 AD) based on documentary evidence, although some of them could actually be archaeophytes. For example, *Agave americana* L. could have been present in the country much earlier than the European conquest (de la Torre et al. 2018), while *Opuntia ficus-indica* (L.) Mill. could have reached Ecuador at any time during the ca. 3000 years of pre-Columbian history of exchanges with Mesoamerican cultures (Ervin 2012). Most of the non-native species, however, reached Ecuador in recent times, with exponential increases around 1910–1920. These years were key for the arrival of goods to the country but also for their introduction inland. The Guayaquil–Quito railway was completed in 1908, which brought sweeping economic and social transformations that contributed decisively to national integration (Esvertit Cobes 2015). It is widely acknowledged that railways contribute to the diffusion of non-native plants from the entry ports (Ascensão and Capinha 2017). The opening of the Panama Canal in 1914 boosted the international maritime trade of Ecuador, which peaked in the period 1919–1920 (Acosta 2006).

Our study shows the Andes as the richest of Ecuador's three bioregions, in terms of total richness (with over 90% of detected taxa) and richness per km^2. This probably explains why temperate Asia is a more prolific donor of non-native plants for continental Ecuador as a whole than tropical Asia, when the opposite was expected (as the whole Amazonian and over three-quarters of the Coastal region have tropical climates in any of their variants, i.e., climates Af, Am, or Aw; https://koppen.earth/). The reasons for the concentration of non-native plants in the Andes could be various and include historic, environmental, and climatic factors, among others. The arrival of the railway to Quito (located in the Andes) in 1908 not only likely favored the spread of non-native species in the Andes, but also boosted the trade and economy of the city (Miño Grijalva 2018), thus contributing to habitat disturbance

(one of the main drivers of invasions; IPBES 2023). The richest natural region regarding non-native taxa—the Andean Shrub, with 368 of the total 486 ones—is one of the most degraded landscapes in Ecuador due to human activity (Sarmiento and Frolich 2002), and today, it is the most densely populated area in Ecuador. Accordingly, the Andes' species accumulation curve has grown exponentially since the 1910s, outpacing slower increases in the Coastal and Amazonian regions. In addition, the Andes' high diversity of regional climates and its rugged terrain have created microclimates that support species with varying climate needs, from arid (e.g., *Aloe vera* (L.) Burm. f., *Cotyledon orbiculata* L.) to wet tropical (*Colocasia esculenta* (L.) Schott, *Musa velutina* H. Wendl. & Drude). Finally, a sample bias may also have a role, as it is well known that mountains have attracted the attention of botanists and naturalists for centuries, including Alexander von Humboldt and Aimé Bonpland who centered their stay in the Andes of Ecuador in 1802 (Romoleroux 2010).

The non-native flora of continental Ecuador is dominated by herbaceous species, particularly by annual/biennial plants. Some studies support the hypothesis that herbaceous species exhibit greater invasiveness than other growth forms (e.g., Omer et al. 2021; Borokini et al. 2023; Sohrabi et al. 2023). This is attributed to their ability to quickly colonize disturbed habitats through rapid and abundant seed production (Baker 1965; Schippers et al. 2001) and their relatively short generation time, which allows them to adapt more swiftly to novel ecological conditions (Compagnoni et al. 2021). Although herbaceous species were over-represented among naturalized taxa compared to casual species in Ecuador, our log-linear models showed no significant association between life form and casual/naturalized status. In our study, this over-representation appears to be an artifact caused by the much larger number of non-native herbaceous species relative to other growth forms.

Naturalized plants in continental Ecuador are significantly associated with longer residence times compared to casual taxa, which aligns with global trends (Milbau and Stout 2008; Pyšek et al. 2009; Rojas-Sandoval and Acevedo-Rodríguez 2015; Schmidt et al. 2017; Gioria et al. 2023). Extended residence times increase propagule accumulation, enhancing the likelihood of population establishment and range expansion (Pyšek et al. 2009). Additionally, evolutionary adaptations to local conditions—often requiring many generations—can improve a species' competitive advantage over native species (Ahern et al. 2010), thus promoting naturalization. Longer residence times also tend to enhance local dominance, as positive feedback between aboveground populations and seed banks strengthens persistence and spread (Aldorfová et al. 2020). Naturalized status is also significantly linked to whether a non-native plant species has any recorded local use in Ecuador. Globally, species cultivated for economic purposes are 18 times more likely to naturalize, especially those used for animal feed or as ornamentals (van Kleunen et al. 2020). Economic plants experience higher propagule pressure due to repeated introductions and secondary releases via cultivation (Kowarik 2003; Guo et al. 2024). In fact, our results suggest that species without a known use are often casual.

Our findings suggest that species with longer residence times often have more uses, as reported in South Africa (van Kleunen et al. 2020; Yessoufou et al. 2022). These studies show a correlation between introduction time and medicinal uses, which in turn are positively associated with the total number of uses. In other words, the longer a given plant has been around, the more uses can be expected to be discovered by the local community (medicinal but also food, construction materials, etc.). However, in Ecuador not all uses correspond to the same residence

time. For instance, ornamental species often have shorter residence times, a trend also observed in eastern Spain (Gómez-Bellver 2023) and the Caribbean (Rojas-Sandoval and Ackerman 2021). Such a pattern is probably caused by changes in the uses of introduced plants through time; more contemporary activities such as urbanization and tourism have driven the introduction of many ornamental plants (Rojas-Sandoval and Ackerman 2021).

Lessons learned from cataloguing the non-native flora of continental Ecuador: a way forward for other megadiverse countries

Global surveys indicate that the megadiverse Neotropics is one of the areas with fewer capacities to prevent and manage species invasions, as a result of a combination of factors such as lack of awareness, lack of cataloguing efforts, or insufficient border controls, among others (Early et al. 2016). However, the present catalogue helped us to uncover the spatial gaps (and, secondarily, other gaps such as the underrepresentation of casual taxa). Then, what emerges from the results is that the non-native flora of continental Ecuador is sharing with other parts of the Neotropics a series of traits as (1) a lower percentage with respect to the total flora (i.e., native plus non-native plants) compared to other latitudes, particularly Europe; (2) a lower percentage of casual plants relative to the naturalized; (3) the predominance of Asia and Africa as the main origin of the non-native species; (4) a total lack of archaeophytes, and (5) significant geographical knowledge gaps (which mostly correspond to the remote Amazonian areas). Most of these traits respond to a series of historical (e.g. a past colonial occupation) but especially socioeconomic factors, including low GDP, low investment in R&D, and large indigenous populations.

Indeed, the low number and density of non-native plant species in Ecuador's Coastal and Amazonian bioregions is partly attributable to limited botanical knowledge, particularly in the Amazonian rainforest (Zenni et al. 2022). Thus, a sizeable increase in the Ecuadorian catalogue of non-native plants and the catalogues of the other megadiverse Neotropical countries (except for Mexico)—as all of them have large portions in the Amazonian rainforest—would be expected once extensive new fieldwork is completed.

Key priorities, thus, should include expanding fieldwork in underexplored regions for the specific case of Ecuador the Coastal but particularly the Amazonian areas. In addition, floristic surveys specifically focused on urban and peri-urban areas (such as those of the Guayaquil, still poorly surveyed) because these areas are often the first entry point for newly introduced plant taxa, and also facilitate the moving of species through each subsequent invasion stage (i.e. "the urban effect"; Potgieter and Cadotte 2020). To achieve this, several CS initiatives can be employed, which have the advantage of requiring minimal or no governmental funding but allow to carry out fieldwork that otherwise would not be possible (López-Guillén et al. 2024). Detecting and inventorying the non-native species through CS experiences has already proven their effectiveness in several areas of the world (e.g. Compagnone et al. 2024; González-Moreno et al. 2024; Pocock et al. 2024) and, if correctly trained and supervised by professionals (Aceves-Bueno et al. 2017; López-Guillén et al. 2024), would play a crucial role in surveying the most unexplored areas by the local people. In Ecuador, iNaturalist projects to survey local flora are showing some promising results, with some projects being implemented since the late 2010s (e.g. Biodiversidad Mitad del Mundo by UEMM, with

high school students that survey the flora and fauna of an area located northern of Quito; https://ecuador.inaturalist.org/projects/biodiversidad-mitad-del-mundo-uemm). iNaturalist has already provided valuable data that has allowed us to include some species in the present catalogue of continental Ecuador (about 30, e.g., *Acacia dealbata*, *Musa velutina*, *Oxalis pes-caprae*, or *Senecio niveoaureus*) and, thus, increasing in the use of this CS-tool in the country (e.g. through projects of volunteers aimed to do fieldwork in poorly surveyed areas, these would mirror the non-native species bioblitzes that are relatively common in the Global North) would produce quick increases in the checklist of non-native species.

Employing CS data in non-native species cataloguing has also other advantages, such as helping to classify species based on their invasion status, distinguishing between wild and cultivated individuals, and, if confirmed as wild, further categorizing them as casual, naturalized, or invasive. iNaturalist was successfully applied to this end for the *Kalanchoe* occurrences in Ecuador a few years ago (Vargas et al. 2022), and it has also been employed herein. Another advantage of using CS data is that it facilitates estimating introduction years, particularly for recent introductions. In recent times, more and more biodiversity observations come from citizen scientists who record species sightings on their phones rather than collecting physical specimens (Eckert et al. 2024). Despite the potential biases that CS data can have such as taxonomic misidentification, errors in georeferencing, and the over-representation of common and abundant species in urban areas, these limitations can be minimized by conducting verification and validation process to ensure data reliability. Recent studies highlight the importance of CS platforms (Mannino and Balistreri 2018; Eritja et al. 2019; Young et al. 2021; Pocock et al. 2024). Indeed, with a growing network of citizen scientists—reflected in the increasing number of observations and their involvement in recent years—CS can facilitate the first detections of non-native species, highlighting its rising value in the early detection of alien species (Encarnação et al. 2021; Compagnone et al. 2024). Despite iNaturalist limitations, this and other CS platforms could play a crucial role in geographic areas such as the Neotropics where the herbaria are rarely digitized, and, in most cases, the specimens labels are not even computerized (Park et al. 2023), so the only way to access specimens is by physically visit the herbaria. This latter, regrettably, is not even possible in Venezuela, where the National Herbarium—one of the largest of the Neotropics—is partially dismantled (Avendaño et al. 2022).

A natural further step in cataloguing the non-native flora of continental Ecuador would be determining which of the naturalized plant taxa should be prioritized in terms of management. The selection of the most impactful species in continental Ecuador is already underway, and is a critical step for policy development. Having official (i.e., national decree) lists of banned invasive non-native species, is a prerequisite to preventing their introduction and regulating their management (Early et al. 2016) that unfortunately, there are lacking in most megadiverse Neotropical countries, including Ecuador (Zenni et al. 2022). In addition, having complete catalogues for each of the countries in a given region (the Neotropics for the present case) allows the implementation of more comprehensive prevention policies. Plants that have not yet been established in a given country but are already invading a neighboring country could be included on a "watch list" or classified as "potentially invasive non-native species", an approach that is mandatory in European Union countries (Genovesi and Shine 2011).

As a concluding remark, our study delivers the most comprehensive inventory of non-native vascular plants for continental Ecuador to date and also

proposes a replicable methodological framework with seven steps for cataloguing non-native plant taxa in megadiverse countries with limited baseline data (Fig. 2). This framework involved five key components: (1) compiling and standardizing occurrence records from multiple secondary sources, including CS portals—an often overlooked source of data; (2) conducting a national expert consultation to validate and classify taxa based on their cultivation and invasion status; (3) organizing training webinars to clarify key concepts and terminology, supported by IPBES experts; (4) verifying doubtful records using georeferenced photographs from CS platforms and complementary tools such as Google Maps; and (5) applying multivariable statistical models to explore ecological and biogeographical patterns. As part of this process, we compiled detailed information for each taxon, including geographic origin, year of first record, life form, lifespan, and documented local uses. This integrative approach allowed us to assess how these factors relate to naturalization status, even in the absence of long-term ecological monitoring (which is the norm in most megadiverse countries). By combining expert-based knowledge, open-access tools, capacity-building efforts, and trait-based data, our framework reduces uncertainty and enhances the quality of taxa inventories. We believe this methodology provides a practical, scalable template for other megadiverse but data-deficient countries to support prevention, early detection, prioritization, and evidence-based management of invasive non-native plants.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

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Supplementary material 1

Non-native wild plant taxa for continental Ecuador detailing the taxonomy, taxa type, life form, life-span, invasion status, locality and year of oldest record, geographic origin, local uses, natural regions, and bioregion

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Data type: xlsx

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Supplementary material 2

Logistic regression model outputs

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Data type: docx

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Supplementary material 3

Frequency of attributes of non-native flora in continental Ecuador

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Data type: xlsx

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Supplementary material 4

Log-linear models outputs

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